8. *The Cranial Structure of the Titanosuchian: Anteosaurus.* By L. D. Boonstra, D.Sc.

(With 22 text-figures.)

Historical

Although the *Anteosaurus* skull was first described by Broom as long ago as 1910, the details of the cranial structure are still very inadequately known.

Watson in 1914 gave some details of the structure of the incomplete skull in the British Museum and in 1921 the same author, giving details of the snout, instituted the name *Anteosaurus* for the specimen hitherto thought to be a *Titanosuchus*.

Broom in 1929 founded an additional species — *A. minor* — on a piece of the skull roof.

Broili and Schröder in 1935 described certain skull fragments under the name *Titanognathus lotzi*.

In 1936 the present author figured and described a distorted skull of *A. minor* that had been sold to the American Museum by Dr. Broom.

In the same year Broom described a good skull and lower jaw under the name *Dinosuchus vorsteri*.

In 1948 the present author published a figure of a skull, which in 1952 was named *A. abeli*, and in 1953 a taxonomic account of the Titanosuchians included a number of photos of *Anteosaurus* skulls in the South African Museum.

Material

The present paper is based mainly on the large number of specimens in the collection of the South African Museum, viz.

S.A.M. 2752. Vivier Siding, Beaufort West. Coll. Haughton & Whaits. Posterior two thirds of the skull without basis cranii.

S.A.M. 4340. Leeurivier, Beaufort West. Coll. Haughton. A good skull, though distorted by a simple shear, with part of the lower jaw.

S.A.M. 5621. Leeurivier, Beaufort West. Coll. Haughton. A snout and part of the skull roof.

S.A.M. 9123. Voëlfontein, Prince Albert. Coll. Boonstra. A weathered skull.

S.A.M. 9139. Voëlfontein, Prince Albert. Coll. Boonstra. A weathered skull fragment.

S.A.M. 9140. Voëlfontein, Prince Albert. Coll. Boonstra. A partial disarticulated skull.

S.A.M. 9329. Kruisvlei, Beaufort West. Coll. Boonstra. A good skull and much of the lower jaw.

S.A.M. 11293. Boesmansrivier, Beaufort West. Coll. Boonstra. A good weathered skull, slightly dorso-ventrally compressed and distorted, with some bones of the occiput disarticulated.

S.A.M. 11296. Kruisrivier, Sutherland. Coll. Boonstra & Laurenson. A very good skull and lower jaw, though somewhat distorted by a simple shear.

S.A.M. 11302. Buffelsvlei, Beaufort West. Coll. Boonstra & Marais. A fair, weathered skull and lower jaw.

S.A.M. 11492. Mynhardtskraal, Beaufort West. Coll. Boonstra. A fairly complete skull without lower jaw.

S.A.M. 11576. Klein-Koedoeskop, Beaufort West. Coll. Boonstra. A snout with fairly well preserved teeth.

S.A.M. 11577. Bulwater, Beaufort West. Coll. Boonstra & Truter. A good practically undistorted three quarters of a well preserved skull.

S.A.M. 11592. Dikbome, Laingsburg. Coll. Boonstra & Du Plessis. A weathered skull, but with a good palatal region.

S.A.M. 11694. Koringplaas, Laingsburg. Coll. Boonstra & Du Plessis. A very good undistorted skull without the lower jaw.

S.A.M. 11929. Kruisvlei, Beaufort West. Coll. Boonstra. The greater part of a skull in intractable matrix.

S.A.M. 11946. Buffelsvlei, Beaufort West. Coll. Boonstra & Marais. A nearly complete, good skull, slightly distorted by a simple shear.

S.A.M. 11949. Nuwefontein, Fraserburg. Coll. Boonstra & Jooste. A partial skull, snout and occiput not in contact.

General Skull Form

There is some difficulty in determining the correct skull form in *Anteosaurus,* due to the post-mortem deformation the available material has usually undergone. In only one skull (S.A.M. 11694) there appears to be little disturbance of the original symmetry. In 8 the deformation is chiefly due to dorso-ventral pressure, but accompanied by some measure of distortion. In 5 specimens the skulls have been subjected to a shearing action — mostly in the form of a simple shear. In these sheared specimens it is of interest to note that they were all lying on their left sides. In only 1 specimen, lying on its right side, the deformation was due almost wholly to compression from side to side.

In the figures the legend indicates where an attempt has been made to correct the effects of the deformation. The resulting correction made from the dorsal and ventral aspect has in some cases not produced the same result and a mean between the two results may indicate the correct condition, but not necessarily so.

The *Anteosaurus* skull is large to very large (480-800 mm. max. length; 222-612 mm. max. width). The snout (with the mandible) is much higher than broad and thus, notwithstanding the width over the temporal region, the skull gives the impression of being high and narrow. This is in sharp contrast to the other Titanosuchians and the Tapinocephalia. In those specimens where the incisors are present the carnivorous nature is strongly evident. The prominent boss-like development of the upper part of the postorbital bar is striking, and in some specimens this rugged appearance is further strengthened by the presence of bosses on the jugal and angular and around the pineal foramen with a lesser or greater amount of swelling of the frons. The great lateral and posterior sweep of the temporal arches is characteristic; the temporal fossa is large and extends far ventrally with a relatively narrow infra-temporal arch. The ventral postero-lateral corner of the skull is not formed by the quadratojugal lying on the surface, but, lying medially, gives an un-Deinocephalian-like appearance to the *Anteosaurus* skull.

The orbits are of medium size and face anterolaterally; the nostrils are non-terminal and lie laterally, whereas in all other Deinocephalians they are directed much dorsally. The intertemporal region is fairly narrow, but without any suggestion of a sagittal crest. The mentum of the lower jaw is high and squarish.

The anterior part of the dentigerous border of the upper jaw sweeps sharply upwards, exposing the long intermeshing incisor teeth.

The lower jaw is hinged fairly far posteriorly.

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a. The Skull in Lateral View (Figs. 1, 6, 8, 11, 17)

In lateral view the skull is roughly pearshaped in outline. The preorbital portion is much longer than the postorbital part. The lateral direction of the nostril, orbit and temporal opening is apparent. The temporal opening extends far ventrally and the infratemporal bar is narrow. The quadratojugal is not a bone of the surface but lies medially of the postero-lateral corner of the skull. The side of the snout is fairly vertical.

The Premaxilla (P.M.) forms the anterior $\frac{1}{4}$ of the upper edge of the skull; anteriorly it has a rounded curve to the dentigerous border, which curves

sharply upwards in antero-posterior direction; from the nostril a groove in the surface of the bone runs anteriorly, lying above the curved premaxilla-maxillary suture; on the lower border of the nostril the premaxilla is separated from the septomaxilla by a narrow tongue of the maxilla; the anterior $\frac{1}{2}$ of the internarial bar is formed by a strong girder of the premaxilla, but in the posterior half the nasal helps in forming the internarial bar;

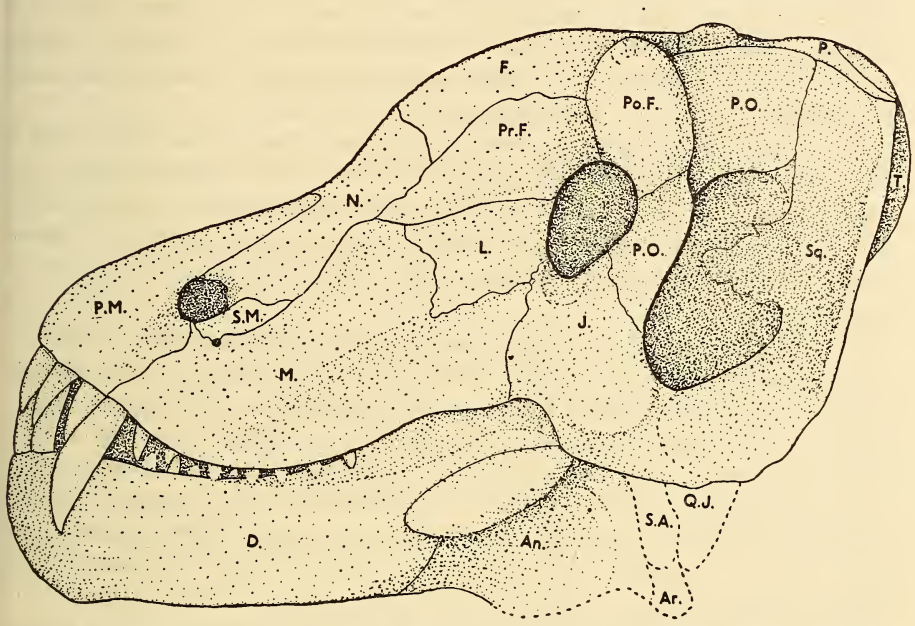

FIG. 1.—*Anteosaurus abeli*. Holotype. S.A.M. 11296. Kruisrivier, Sutherland. Lateral view of the left side of the skull. ($\times \frac{1}{6}$.) The distortion due to a simple shear corrected. In this and all the other figures, orthoprojections, obtained with a pantograph, are given. In the lateral views the projection is on the median plane. In the dorsal and ventral views the projection is on the plane in which the postcanines lie. In the occipital views the projection is at right angles to the plane of the postcanine alveolar border.

An.—angular; Ar.—articular; B.O.—basioccipital; B.S.—basisphenoid (sheathed by parasphenoid); D.—dentary; E.O.—exoccipital; F.—frontal; I.P.—interparietal; J.—jugal; L.—lacrimal; M.—maxilla; N.—nasal; P.—parietal; Pal.—palatine; P.M.—premaxilla; P.O.—postorbital; P.O.c.—paroccipital; P.V.—prevomer; Po.F.—postfrontal; Pr.F.—prefrontal; Pt.—pterygoid; Q.—quadrate; Q.J.—quadratojugal; S.A.—surangular; S.M.—septomaxilla; S.O.—supraoccipital; Sq.—squamosal; St.—stapes; T.—tabular; Tr.—transversum.

posteriorly the premaxilla has a wedge-shaped prolongation into the nasal, extending posteriorly of the nostril roughly for the length of the nostril, or in some cases for double this length. The premaxilla is either edentulous or carries a variable number of incisor teeth (1-5), with the number sometimes varying in the two premaxillaries of the same skull. There is a considerable variation in the length of the dentigerous border of the premaxilla, even within what I consider to be the same species; this variation is concomitant

with both the number and size of the incisor teeth; in *A. abeli,* S.A.M. 4340, the dentigerous edge on the left side with 5 incisors is 160 mm., whereas in S.A.M. 11296 with 3 teeth it is 90 mm., and in the right size with 4 teeth it is 110 mm.

The Septomaxilla (S.M.) has a small facial exposure; dorsally it forms the posterior part of the lower narial border; curving sharply inwards it extends to near the median line to form the floor of the nostril. Anteriorly it does not meet the premaxilla, being separated from this bone by a narrow tongue of the maxilla. Posteriorly it extends as a short wedge in between the nasal and maxilla. There is a small septomaxillary foramen.

The Nasal (N.) is in lateral view seen to be a long narrow bone with a constricted waist. Anteriorly it forms the posterior border of the nostril, with a dorsal prong extending in to the dorsal narial border and a ventral prong extending in to the ventral narial border. Posteriorly it extends to about halfway the swelling of the forehead, where it meets the frontal in a feebly sigmoid suture.

The Maxilla (M.) is a large bone extending far posteriorly, where it overlaps the jugal. In the smaller forms, e.g. *A. cruentus* (S.A.M. 11694), it does not in its ventral part stretch so far posteriorly as in the larger forms, so that in the former the suture with the jugal is oblique, whereas in the latter it is vertical. On the surface of the maxilla there is a strong ridge running obliquely from the orbit in the direction of the canine. In its dorso-posterior part the maxilla has a triangular tongue which separates the jugal from the lacrimal except for a short distance near the orbit. The maxilla carries a variable number of teeth (5-8), often irregularly spaced.

The Frontal (F.) forms in lateral view the middle portion of the dorsal edge of the skull. It forms the major portion of the fore-head swelling, as this is varyingly developed in the different forms. The frontal has a small tonguelike entry into the dorsal orbital border, except in S.A.M. 11296 where the large postfrontal boss overlaps it.

The Prefrontal (Pr.F.) has in lateral view a curved dorsal edge and a fairly straight ventral edge. Anteriorly it stretches as a wedge between the nasal and maxilla, and posteriorly it forms the thickened anterodorsal part of the orbital border. It forms the lateral part of the forehead swelling and, where this is great, it forms an overhanging bulge.

The Lacrimal (L.) varies in size, due to the extent to which the maxilla extends posteriorly. It is a roughly quadrilateral bone with a short suture with the jugal and forming the anterior part of the orbital border. Its suture with the prefrontal lies on a fairly sharp ridge.

The Jugal (J.) is quite a large bone notwithstanding the encroachment of the maxilla anteriorly. It forms the lower orbital border and extends a little on to the anterior as well as the posterior orbital border. It has only a small

contact with the lacrimal. Entering the postorbital bar it is greatly overlapped by the postorbital. It has a long and strong posterior process which, in the form of a sheet of bone, forms the inner surface of the zygomatic arch and extends posteriorly to past the quadratojugal. The outer surface of the process is overlapped by the zygomatic process of the squamosal. The amount of this overlap varies in the different forms. In *A. cruentus* (S.A.M. 11694) the outer surface of the jugal, below the orbit, is fairly smooth, except for a hollow which is present in all forms immediately below the orbital border, but in the larger forms there is a swelling, feeble in *A. abeli* (S.A.M. 4340), low in *A. abeli* (S.A.M. 11296) and *A. vorsteri* (S.A.M. 11577) and strong and prominent in *A. crassifrons* (S.A.M. 11946 and S.A.M. 11302) and *A. acutirostris* (S.A.M. 9329) where it forms a prominent overhanging outgrowth.

The Postfrontal (Po.F.) forms the large and prominent boss-like growth overhanging the postero-dorsal orbital border. The size of this boss determines the amount of its overgrowth over the surface of the frontal and the size of the entry of the frontal tongue into the dorsal orbital border. Ventrally the extent of the pachyostosis in the postfrontal determines the degree to which it overlaps the postorbital on the postorbital bar so that the position of the postfrontal-postorbital suture shows a considerable variation. In the forms where the thickening of the frontal is not very great the postfrontal forms part of the dorsal outline of the skull when observed in lateral view; in the other forms it nearly reaches the dorsal edge or lies well below it.

The Postorbital (P.O.) presents, in lateral view, two distinct surfaces. The more lateral surface is exposed where the bone forms the fairly weak and narrow curved part of the postorbital bar overhung to a greater or lesser extent by the bosslike postfrontal. In a more medial plane the postorbital provides the sheet of bone which forms the lateral face of the intertemporal region and forms the dorsal edge of the temporal fossa. There is a considerable variation in the size and shape of this plate of bone. Posteriorly it meets the upsweeping arm of the squamosal in a long suture. Ventrally its edge overhangs the squamosal where this bone forms the inner face of the temporal fossa.

The Parietal (P.) is in lateral view seen only where it presents the lateral surface of the pineal boss and its long postero-lateral tongue intercalated between the squamosal and tabular. It does not form the upper inner face of the temporal fossa as it is here covered by the postorbital which forms the inner face of the fossa.

The Tabular (T.) in lateral view is seen to form the postero-dorsal border of the posttemporal arch and in some forms the tabular is also seen as it

descends on the posterior surface forming the prominent ridge limiting the occiput proper.

The Squamosal (Sq.) is a large bone of intricate shape. In lateral view it is seen to form the lateral part of the posttemporal arch and the greater part of the inner surface of the temporal fossa, except for that part formed by the postorbital, and the outer surface of most of the zygomatic arch. Anteriorly it meets, within the temporal fossa, the postorbital, and lower down the supraoccipital and paroccipital. In the angle between the zygomatic process and the inner facing of the temporal fossa the squamosal also forms the niche in which the upper and hinder faces of the quadrate are housed.

The Quadratojugal (Q.J.) is not preserved in most of the specimens, but in the four skulls in which it is preserved, its lateral surface appears to be triangular in outline and this does not lie on the surface of the postero-ventral outer corner of the skull as it does in all other known Deinocephalia, but lies in a plane medial to the subtemporal arch as in Therocephalians, Gorgonopsians, and the higher Therapsids. The quadratojugal rests on a ledge of the quadrate above the outer quadratic condyle. In these relations it approaches very closely to the condition recently described by me in the contemporary Pristerognathid Therocephalians. In one skull of *A. cruentus* (S.A.M. 11694) there is a small notch in the squamosal lying lateral to the quadratojugal.

Palatal bones. When the lower jaw is disarticulated the lateral surfaces of some of the palatal bones are seen. The lateral surface of the lateral flange of the pterygoid (Pt.), the quadrate ramus of the pterygoid and of the anterior pterygoid process, the transversum and palatine are all visible. In *A. cruentus* (S.A.M. 11694) the basisphenoid is also partly seen.

Noteworthy are the strong and deep pterygoidal flange and the prominent dentigerous boss on the palatine.

b. The Skull in Dorsal View (Figs. 2, 7, 9, 10, 14, 18, 21, 22)

In dorsal view the *Anteosaurus skull* presents in outline a pear-shaped form, with the jugal bosses in some forms appearing as lateral protuberances, in some cases low and in others prominent. In *A. crassifrons* the skull is short and squat with a relatively broad snout. In the others the snout is either narrow, fairly narrow or moderately wide. The forehead swelling is low, moderate to very massive. In all the postfrontal boss on the dorsal part of the postorbital bar is prominent. In *A. acutirostris* (S.A.M. 9329) and *A. crassifrons* (S.A.M. 11946) the jugal boss protrudes strongly beyond the general skull-outline; in *A. abeli* (S.A.M. 11296) and *A. vorsteri* (S.A.M. 11577) moderately, and in the others not at all.

The orbits are in all cases only partly visible, being overhung by the fore-head swelling; in *A. cruentus, A. abeli* and *A. vorsteri* this overhang

is least, in *A. levops* and *A. acutirostris* fairly great and in *A. crassifrons* very great.

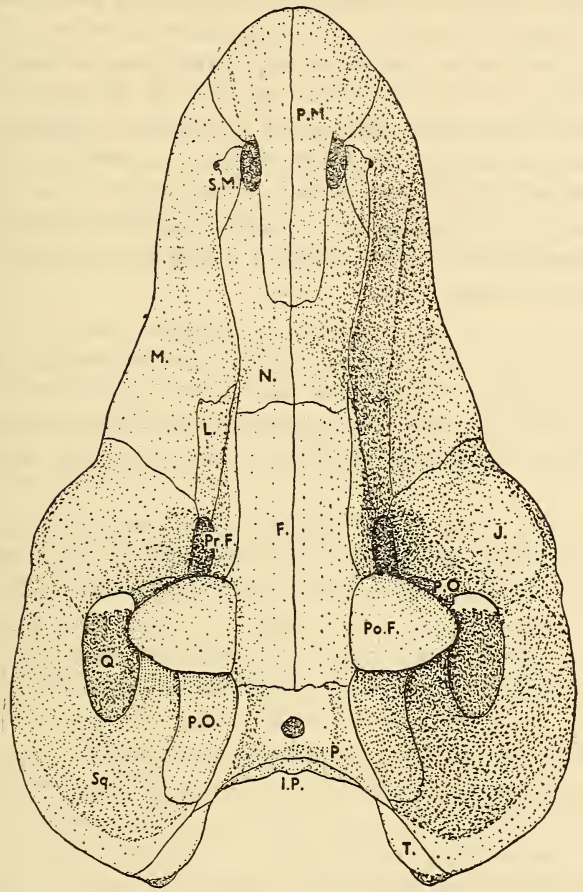

FIG. 2.—*Anteosaurus abeli*. Holotype. S.A.M. 11296, Kruisrivier, Sutherland. Dorsal View with distortion due to a simple shear corrected. ($\times \frac{1}{6}$.)

The temporal fossa is broad and long with the temporal arches flaring greatly laterally and posteriorly. The occipital edge is deeply concave from side to side. The intertemporal region is generally flat, but with a pineal boss varying from low to prominent and massive. The intertemporal width is small, medium to fairly broad with no suggestion of the development of a sagittal crest. The pineal foramen is fairly small and situated near, to very near, the occipital edge. The internarial bar is strong and massive.

The Premaxilla (P.M.). The two premaxillaries together form the rounded anterior margin of the skull. Laterally they meet the maxilla in a curved

suture lying lateral to a groove in the premaxillary surface. The premaxilla forms the anterior and most of the dorsal narial border. Together they form a stout internarial bar, which, extending backwards for only a short distance, is posteriorly abruptly truncated. This truncation is rather surprising since the premaxilla-nasal suture lies in a groove which is continued to near the fronto-nasal suture. This accounts for the error of observation on my part as depicted in the figure of the specimen in the American Museum, which later in this paper is made the type of a new species, *A. minusculus*.

The Septomaxilla (S.M.) is as already described in lateral view.

The Maxilla (M.), in addition to the features described when seen in lateral view, shows clearly that the suture between it and the septomaxilla and nasal lies along a curved ridge.

The Nasal (N.). The paired nasals are hourglass-shaped in outline, with the truncated posterior end of the premaxillaries separating them in their anterior half to a third. The posterior part of the nasals enters the fore-head swelling to a greater or lesser extent depending on the development of this thickening. Where the frontal swelling is least, the nasal extends furthest posteriorly.

The Frontal (F.). The paired frontals form a more or less pronounced cruciform figure with the narrow tongues entering the orbital borders forming the cross member. In two cases this cross member is truncated and on the surface does not enter the orbital border. The postfrontal boss overflows on to the frontal surface to a varying extent. Posteriorly the frontals meet the parietals in a suture running across the skull just anterior to the pineal boss, but in *A. crassifrons* the pineal boss extends anteriorly as a strong swelling on to the posterior part of the frontals. The frontals meet the edge of the postorbitals posterior to the limits of the postfrontals.

The Prefrontal (Pr.F.). In dorsal view the extent to which the prefrontal enters the fore-head swelling is indicated in the figures. Where this swelling is least developed the overhang of the prefrontal over the orbit and the lateral skull face immediately anterior to the orbit is least and the transition from the dorsal to the lateral surface not very abrupt. Whereas in *A. crassifrons* the swollen prefrontal all but obscures the lacrimal from dorsal view.

The Lacrimal (L.) is as described in lateral view, except that in dorsal view it is overhung by the prefrontal swelling to a greater or lessor extent depending on the amount of the pachyostosis of the prefrontal.

The Postfrontal (Po.F.). In dorsal view the knob-like bosses formed by the greatly thickened postfrontals are a very prominent feature. In most skulls this boss completely overhangs the part of the postorbital entering the postorbital bar; in others the lower part of the postorbital above the suture with the jugal is visible, and in three cases the boss leaves exposed, behind

its posterior edge, the postorbital as it sweeps from the upper temporal face down to the lower part of the postorbital bar.

The Parietal (P.) has a relatively small dorsal surface. The two bones are fused except where they are pierced by the fairly small pineal foramen. Round the pineal foramen the parietals are thickened to form a boss variable in size and shape. In some skulls a distinct ring wall with sharp edges surrounds the foramen, in others only a low mound is formed, whereas in *A. crassifrons* a massive thickening extends into the frontals and in *A. vorsteri* (S.A.M. 11577) the frontal surface, anterior to the low boss, is slightly hollowed out in the form of a V shaped depression bounded by a low ridge. In one specimen (S.A.M. 2752) the pineal boss overhangs the occiput. The pineal foramen is near or very near the posterior edge of the parietals.

Posteriorly each parietal sends out a long horn with its end wedged in between the dorsal end of the tabular and the upper part of the squamosal. The outer edge of the parietal horn forms a sharp ridge lying lateral to a groove and thus sharply demarcating the intertemporal surface.

The Postorbital (P.O.). The posterior flange of the postorbital is a large sheet of bone applied to the outer surface of the parietal and, extending far back, it is met by the upsweeping squamosal. The ventral edge of the postorbital flange overlaps and overhangs the antero-medially directed sheet of the squamosal.

Little of that part of the postorbital which helps to make up the postorbital bar is usually seen in dorsal view, being overhung by the greatly swollen postfrontal.

The Jugal (J.). In dorsal view the boss of the jugal, in those forms where it is developed, is shown very clearly as it determines the outline of the skull in this region.

The Squamosal (Sq.) in dorsal view presents a zygomatic process covering the latero-dorsal surface of the long zygomatic process of the jugal. From this level the squamosal sweeps upwards to form the postero-lateral part of the posttemporal arch, where it meets the postero-laterally sweeping horn of the parietal and posteriorly abuts against the tabular. Within the temporal fossa the squamosal forms its large internal surface; dorsally meeting the postorbital and, at a lower level, sweeps antero-medially to meet the supraoccipital and paroccipital. Between the zygomatic process and the antero-medial process a niche in the anterior squamosal surface houses the quadrate.

The Interparietal (I.P.), and *Supraoccipital* (S.O.). In dorsal view little of the occiput is seen as this is vertical. The dorsal edge of the interparietal and in some cases a bit of the surface of the supraoccipital can be seen, and in *A. acutirostris* the occipital condyle.

c. The Skull in Ventral View (Figs. 3, 13, 15, 16, 19)

In general terms it may be said that in the ventral aspect of the skull two surfaces are shown meeting in an obtuse angle at the plane of the transverse pterygoid flanges. Posterior to the very prominent transverse pterygoid flanges the *basis cranii* lies in a more or less horizontal plane, whereas anteriorly the palate is in anterior direction directed upwards. This is accentuated by the upward retreat of the alveolar border of the premaxillaries. The most prominent features in the ventral aspect of the skull are: the strong and deep lateral flanges of the pterygoid, the strong reniform dentigerous bosses of the palatines, the retreat of the alveolar border

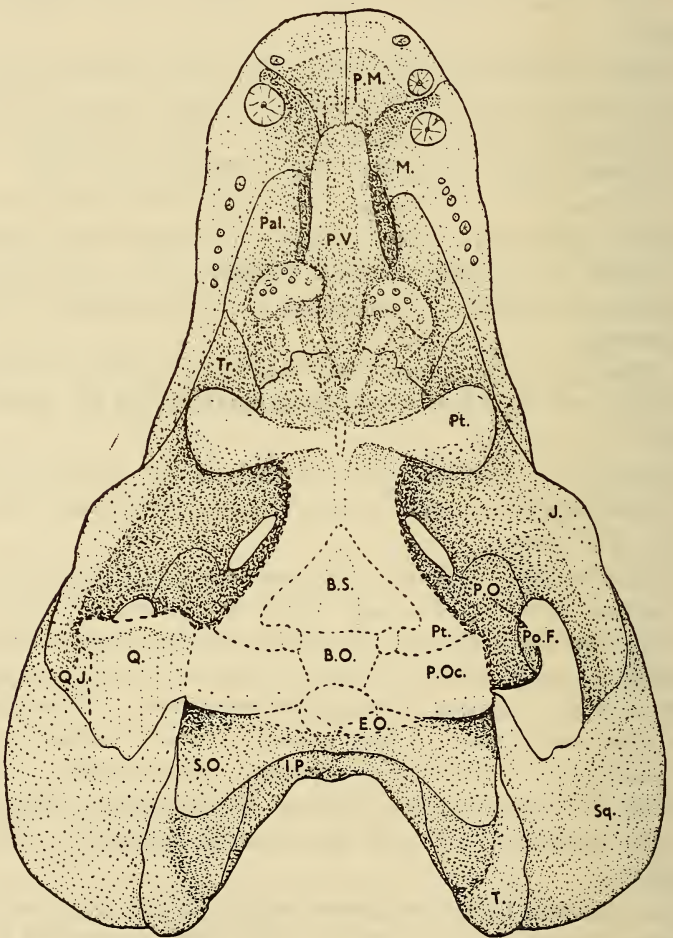

FIG. 3.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Ventral View. (× $\frac{1}{6}$.)

of the premaxillaries, the medial shift of the quadratojugal away from the lateral surface of the skull and the deeply concave occiput.

The Premaxilla (P.M.) has an alveolar border and a palatal process. The alveolar border has retreated upwards. It carries a variable number of teeth — 5, 4, 3. The number of incisors in the two premaxillaries of the same skull is, in some cases, unequal. Where no teeth roots are preserved there is a groove in the alveolar surface which is either clearly separated into separate alveoli, or not. The palatal process meets the prevomers which underly it, and laterally meet the maxilla along a curved suture.

The Maxilla (M.). Ventrally the maxilla has, in addition to its alveolar edge, a medially directed tongue which separates the premaxilla from the palatine and except in *A. crassifrons* makes contact with the prevomer. Antero-medially of the upper canine the maxilla is deeply excavated to receive the fang of the lower canine. The maxilla carries a large canine and a variable number of postcanines. The latter are irregularly spaced and vary in size and in number (5-8). The root cross-sections show the postcanines to be rather feeble teeth of no great functional importance.

The Prevomer (P.V.). The pair of prevomers form a strong interchoanal bar, anteriorly underlying the palatal process of the premaxillaries and posteriorly tapering in between the palatines to make a small contact with the pterygoids. The interchoanal bar is, except anteriorly, deeply excavated longitudinally and each prevomer has a well defined ridge on its lateral edge, which forms the medial border of the slitlike choanae.

The Palatine (Pal.) meets the maxilla in a long suture lingually of the alveolar border and curving upwards forms most of the lateral and posterior border of the choana. Further back it carries a strong and prominent reniform dentigerous boss. In most cases the fair-sized recurved teeth are implanted in a single curve but in *A. vorsteri* (S.A.M. 11577) there appears to be a double row. Posterior to the boss there is a ridge continued on the pterygoid towards the interpterygoidal slit.

The Transversum (Tr.), composed of a sheet of bone lying antero-laterally of the pterygoid flange, meets the palatine, maxilla and jugal and descending along the front and side of the pterygoid flange forms the upper part of the lateral and part of the anterior face of the strong lateral pterygoid flange. There is no fenestra between the transversum and palatine.

The Pterygoid (Pt.) has the usual complex form of the Therapsids. The anterior process is short, the lateral flange deep and strong, the quadrate process sweeps backwards with a straight outer edge and in the middle line the pterygoids together form a fairly deep keel posterior to the interpterygoidal slit. In the fork between the two quadrate rami the pterygoids meet the basisphenoid (basi-parasphenoid) in a U-shaped suture with no development of basipterygoid processes.

In most skulls the posterior extremity of the quadrate ramus is not adequately preserved and its relations with the quadrate uncertain. But in a specimen which I believe to be an *A. crassifrons* (S.A.M. 11929) it would appear that the quadrate ramus of the pterygoid is applied to the inner face of the quadrate a little below the distal end of the stapes. If this observation is correct then the condition is very similar to that in *Jonkeria* and in the Tapinocephalids generally.

The Basisphenoid (B.S.) is apparently sheathed along its under surface by the parasphenoid and presents a ventral surface cup-shaped in outline. Just behind the median pterygoidal keel the median basisphenoidal surface is excavated to form a broad groove, which is continued in the basioccipital right up to the condyle. Lateral to the median groove the basisphenoid develops a rounded ridge which broadens posteriorly until it is posteriorly notched and develops a latero-posteriorly directed tongue, which forms the antero-ventral border of the *fenestra ovalis*. The basioccipital-basisphenoidal suture runs across the median groove from notch to notch. The basisphenoidal-pterygoid suture runs along the lateral border of the rounded basisphenoidal ridge.

The basisphenoid is a short bone, but in *A. major* (S.A.M. 11293) it is nearly twice as long as in all the other skulls.

The Basioccipital (B.O.) forms the greater part of the rounded condyle with the exoccipitals forming the postero-lateral corners. In *A. crassifrons* and *A. acutirostris* the exoccipitals are intimately fused to the basioccipital to form a rounded condyle. Anterior to the condyle the under surface of the basioccipital is in its median part hollowed out to form a wide groove which is continued on to the basisphenoid. The vertical plate of the basioccipital anterior to the condyle reported by Broom in *A. vorsteri* is not shown in any of the skulls I have examined and this incorrect statement can thus only be due to an error in observation. Antero-laterally the corner of the basioccipital is bent sharply downwards to form the strong medial border of the *fenestra ovalis*. Postero-laterally the continuation of this prominent ridge round the *fenestra ovalis* is formed by the antero-medial corner of the paroccipital, which has a similarly bent down process. The basioccipital abuts against the paroccipital in a diagonal line of contact.

The Exoccipital (E.O.), besides forming the postero-lateral corner of the condyle, has a lateral process which overlaps the paroccipital and supraoccipital, but is not very clearly shown in any of the skulls examined.

The Paroccipital (P.O.) forms a stout girderlike bone medially butting against the basioccipital and distally applied to the inner face of the quadrate and making contact with the descending sheet of the squamosal. The dorso-lateral corner of the paroccipital bounds the post-temporal fossa, which is anteriorly closed by the sheet of the squamosal forming the inner lining

of the temporal fossa. Dorsally the paroccipital lies against the lower edge of the supraoccipital.

The Jugal (J.) in ventral view shows its inner surface. Its zygomatic process is here clearly seen to extend far backwards and to form the inner part of the arch, whose outer half is formed by the overlapping zygomatic process of the squamosal.

The Squamosal (Sq.) shows its posterior surface as it sweeps downwards to overlap the posterior face of the quadrate and quadratojugal.

The Quadrate (Q.) and *Quadratojugal* (Q.J.). In most of the skulls studied the quadrate complex is missing. It would appear that it fits rather loosely in the notch of the squamosal in which its upper end is housed. There was apparently also little ankylosis in the joint between the paroccipital and the quadrate. The quadrate and quadratojugal form an antero-posteriorly flattened mass of bone carrying two moderate condyli on its lower edge, which lies somewhat diagonally in the skull, with the outer condyle furthest posteriorly. The quadratojugal is small and resting on a ledge above the outer quadrate condyle is applied to the outer edge of the quadrate. It lies well medial of the lateral edge of the skull and is not a bone of the lateral surface as it is in all other known Deinocephalia.

d. The Skull in Occipital View (Figs. 4, 20)

The occiput is vertical, but deeply concave from side to side. The strong tabular ridges bound the occiput proper laterally. Lateral to this ridge lies the posterior surface of the posttemporal arch, and the groove which in higher Therapsids functions as an auditory groove.

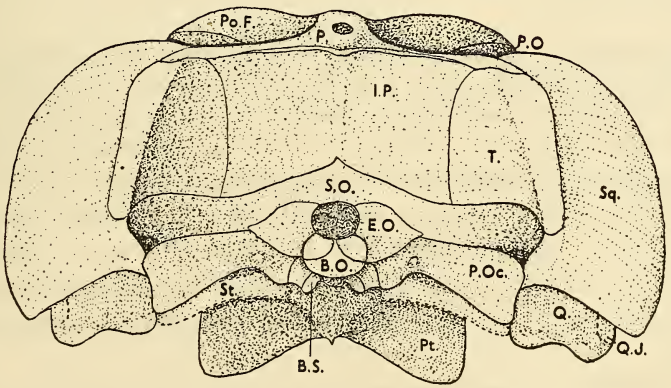

FIG. 4.—*Anteosaurus laticeps*. Sp. Nov. Holotype. S.A.M. 11592, Dikbome, Laingsburg. Occipital View. The possible dorso-ventral compression not corrected. The dorsal part and the quadrate-complex restored from all the other material. ($\times \frac{1}{6}$.)

The Squamosal (Sq.) is seen to form the lateral margin of the skull. Dorsally the squamosal and tabular clasp the extremity of the parietal horn. Ventrally the squamosal overlaps the quadrate and quadratojugal. Medially it makes contact with the tabular in the "auditory groove", which lies lateral to the strong tabular ridge. This ridge is ventrally continued on the squamosal as it fades out. This ridge thus differs materially from the ridge in *Jonkeria*, where the tabular, squamosal and paroccipital contribute to its formation.

The Tabular (T.) carries the strong ridge which forms the inner border of the "auditory groove" and laterally limits the occiput proper. Externally the tabular ridge appears to be sheathed by a thin bone, which I thought may represent the supratemporal, but a number of cross sections in one skull have yielded no evidence to substantiate this. From the ridge the tabular extends medially as a sheet of bone to meet the interparietal. In its dorsal part the occiput consists of 3 layers of bone viz. anteriorly there is a sheet of the squamosal applied to a sheet of the parietal and this is posteriorly covered by the tabular laterally and the interparietal medially.

The Interparietal (I.P.), as a large thin sheet of bone with a ridge in the median line, forms the upper and middle part of the occipital surface.

The Supraoccipital (S.O.) lies below the interparietal and tabular and forms the upper border of the foramen magnum and, laterally, the upper border of the depression which represents the post-temporal fenestra now anteriorly closed by the overgrowing sheet of the squamosal within the temporal fossa. Lateral to the foramen magnum the supraoccipital is overlapped by the exoccipital.

The Exoccipital (E.O.) is seen to form the dorso-lateral segment of the condyle and its lateral flange overlaps the supraoccipital and paroccipital for a short distance.

The Paroccipital (P.O.) is a stout bar between the quadrate and the basioccipital. In posterior view it is clearly shown how its proximo-ventral corner is bent sharply downwards to form the posterior part of the prominent rim of the *fenestra ovalis*. Similarly the downwardly directed processes of the basioccipital and basisphenoid forming the median part of the rim of the *fenestra ovalis* are clearly seen in occipital view. The median groove in the ventral surface of the basioccipital and basisphenoid is also evident.

Stapes (St.) is only partly preserved in one of the skulls studied. It appears to be a stout rod-like bone similar to that of other Deinocephalians but longer.

The Quadrate (Q.) and *Quadratojugal* (Q.J.). In posterior view it is very clear that the quadratojugal has shifted in medial direction as in the higher Therapsids and is no longer a bone of the outer lateral surface of the skull as it is in all other known Deinocephalia.

The Pterygoid (Pt.). In occipital view the deep lateral flanges of the pterygoids are well shown.

The Post-temporal Fenestra does not penetrate the occipital plate as it is anteriorly closed by a sheet of the squamosal. In occipital view it is thus only evident as a depression lying in the corner between the supraoccipital, paroccipital and squamosal.

e. The Lower Jaw (Figs. 1, 5, 6)

Since the quadrate has not shifted much in anterior direction the lower jaw is long. The mandibular ramus is strong and heavy, particularly in its anterior part. In all the larger forms there is a strong and prominent boss on the anterior part of the angular. Unfortunately no lower jaw is preserved in those forms without a jugal boss, but I think it likely that in these cases no angular boss will be developed. In contradistinction to the condition in other Deinocephalia there is in *Anteosaurus* some indication of the development of a low coronoid process to the dentary.

In my material only the outer surface of the mandible is shown exposing the dentary, angular, surangular and articular.

The Dentary (D.) is a massive bone. The mentum is high and fairly upright and the symphysis strongly ankylosed. Posteriorly the dentary curves upwards to form a low incipient coronoid process. The dentary carries a strong canine and a variable number of incisors and postcanines. The number of incisors varies from 2 to 4. The number of postcanines is difficult to determine but seems to vary from 4 to 7.

The Angular (An.) is remarkable for the development on the outer surface of a large egg-shaped swelling in its anterior part. Posterior to the boss the angular has the typical Therapsid structure.

The Surangular (S.A.) is in outer view the typical curved girder-like bone it is in Therapsids generally, but anteriorly it rises and meets the dentary in the low coronoid process.

The Articular (Ar.) has only a small external face forming the extreme postero-ventral corner of the lower jaw.

f. The Dentition (Figs. 1, 5, 6)

The dentition of *Anteosaurus* is clearly that of a specialised type of carnivore. With the large canines, long intermeshing incisors, and feeble postcanines it obviously did no chewing and very little shearing, but was rather well adapted for grabbing and then tearing flesh from its victim, and just before deglutition the lump of flesh was held by the recurved teeth situated on the palatine bosses.

The Anteosaurus-incisors are quite distinct from those in the other carnivorous Therapsids, as for example those usually present in the Therocephalians Gorgonopsians and Cynodonts. In the latter the upper incisors in occlusion lie labially of the lower incisors, whereas in *Anteosaurus* the two sets intermesh as do the herbivorous teeth of the Tapinocephalia. To give the long incisors functioning space the alveolar border of the premaxilla retreats and the upper incisors are directed much anteriorly. The first incisor is smaller than the second and with its fellow forms a distinct pair, as is also the case in the Pristerognathid Therocephalians. This pair passes in between the number one pair of incisors of the dentary. When fully developed there are five upper and four lower incisors, but even in the same skull the number in the two halves is mostly different. So we have, in S.A.M. 11576, 5 left upper, 4 right upper and in both sides 3 lower; in S.A.M. 11296, 3 left upper, 4 right upper and 2 lower on both sides; in S.A.M. 4340, 5 left upper, 4 right upper and 4 left lower; in S.A.M. 11694 no uppers; in *crassifrons* no uppers; in S.A.M. 11577, 2 left and 1 right upper; in S.A.M. 11492, 3 left and no right uppers. In those cases where no incisors or incisor roots are preserved there is in the alveolar border a more or less

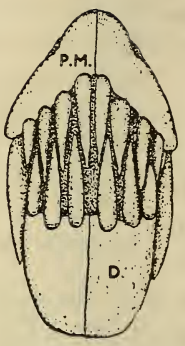

FIG. 5. — *Anteosaurus abeli*. Referred specimen. S.A.M. 11576, Klein-Koedoeskop, Beaufort West. Orthoprojection of the snout on to the plane of the occiput. (× ⅛.)

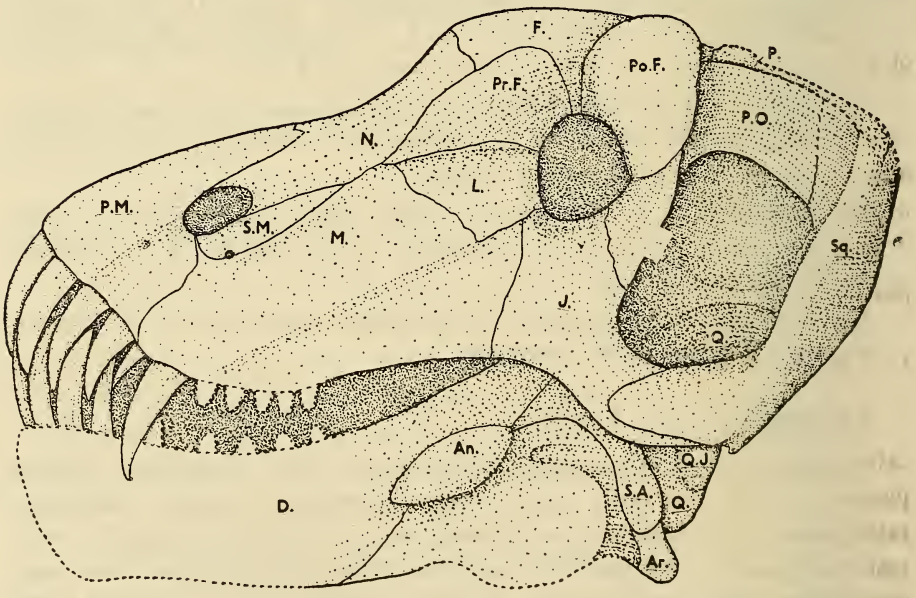

FIG. 6.—*Anteosaurus abeli*. Paratype. S.A.M. 4340, Leeurivier, Beaufort West. Lateral View. (× ⅛.)

distinct groove which in some shows more or less indefinite subdivision into separate alveoli. Without sectioning it is difficult to determine whether some forms were permanently edentulous (rather improbable) or whether the first set has not yet erupted or whether the last set has been shed or whether an antecedent set has been shed and a succeeding set not yet erupted.

In S.A.M. 11296 the left canine is on the point of being shed and the cusp lying posterior to it may be the replacing canine as it does not have the appearance of a postcanine.

The postcanines are not well shown and we usually only have the section of the roots on which to base a count. In S.A.M. 11529 some crowns are well preserved and here the last tooth is a fairly small tooth, 16 mm. long, linguo-labially compressed with diameters 11 and 7 mm. In outline the postcanine is fairly bluntly conical. The postcanines are usually irregularly spaced. Their number sometimes varies in the two maxillaries of the same skull. In the genus the postcanines vary in number from 4 to 8 in the upper jaw.

Taxonomic

In 1921 Watson established the genus *Anteosaurus* on the grounds that a skull in the British Museum (R. 3595) from Tamboerfontein differed from all hitherto known Deinocephalians in the possession of only three incisor teeth and in being the first known Deinocephalian skull in which the upper part of the postorbital bar was strongly swollen to form a very prominent boss.

Subsequent finds have shown that in a series of skulls with the typical boss the number of incisors varies and I propose that as diagnostic character for the genus *Anteosaurus* we should consider only the presence of the typical boss formed by the prefrontal bone.

Accepting this character as diagnostic we have to exclude from the genus *Anteosaurus* the form named *A. minor* by Broom who says of it, "but differs in having only a small thickening instead of a huge boss in the postfrontal region". For this unsatisfactory type, consisting of only the interorbital and intertemporal regions, nomenclatural procedure thus compels one to propose a new generic name. I therefore propose that the skull fragment from Merweville, British Museum (Natural History) R.5742, be known under the generic name *Pseudanteosaurus* gen. nov., genotype *Pseudanteosaurus minor* (Broom).

The specimen in the American Museum of Natural History stated by Broom to be the topotype of the above has, however, well developed bulbous swellings in the upper part of the postorbital bar and must be retained in the genus *Anteosaurus* of which it then constitutes a new species to be named and described later in this paper.

Broili and Schröder's genus *Titanognathus* was based on the following diagnostic characters: "Schädel mit schmaler und steil vom prämaxillaren Kieferrand aufsteigender Schnauze, sehr gross. Praemaxillarer Kieferrand gegenüber dem maxillaren stark in die Höhe gezogen, Symphysenregion des Unterkiefers entsprechend erhöht gegenüber dem rückwärtigen abschnitt des Dentale. Zahnformel: i.$\frac{5}{4(?)}$, c.$\frac{1}{1}$, p.c.$\frac{6}{3+?}$." Restudy of the genotype together with the additional material now known has established that the retreat of the premaxillary edge occurs in *Anteosaurus* and the above dental formula is also within the limits of the genus. The generic name *Titanognathus* thus becomes a synonym of *Anteosaurus* but we may continue to regard this specimen as specifically distinct from the genotype *A. magnificus* under the name *A. lotzi* (Broili and Schröder).

Broom's genus *Dinosuchus* was established on the following diagnostic characters: presence of a dentigerous palatine boss, low position of temporal arch, great width of occiput, large size, dental formula i.4, c.1, p.c.5, huge angular boss. In the large number of skulls now known to fall within the limits set for the genus these above characters are present and any difference in degree cannot be more than of specific value. *Dinosuchus* thus becomes a synonym of *Anteosaurus* and the points in which Broom's specimen differs from the genotype warrant the retention of Broom's specific name, *vorsteri*.

Specific descriptions of the known and new species can now be given:

Anteosaurus magnificus Watson.

Broom, R. 1910. *Titanosuchus ferrox* Owen (in errore).
Watson, D. M. S. 1914. *Titanosuchus ferox* Owen (in errore).
Watson, D. M. S. 1921. *Anteosaurus magnificus* Watson.

Genotype. Incomplete skull. British Museum (Natural History) R. 3595. Tamboerfontein, Beaufort West. Coll. Seeley.

In the type skull the snout was not in contact with the rest of the skull and in his restoration Watson failed to realise that the premaxillary edge curved upwards. This feature of the Anteosaurus skull was first reported by Broili and Schröder and confirmed in all subsequent specimens. Due to the incompleteness of the type skull only an incomplete description can be given for the species viz.:

Skull large; maximum length about 660 mm. Snout long, fairly high and wide. Intersquamosal width not great (360? mm.). Postfrontal boss huge and prominent. Jugal and angular bosses unknown. Fronto-naso-prefrontal swelling fairly weak. Pineal boss prominent with sharp circular border, situated very near occipital edge. Degree of upward inclination of premaxillary edge uncertain. The occiput is fairly high, fairly wide, deeply

concave with a great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises well above the plane of the intertemporal surface. Palate probably long.

Basis cranii unknown. Condyle unknown. Watson gives the upper teeth as i.3, c.1, p.c. 8 on both sides, but Broom states that there may be 5 incisors.

Anteosaurus lotzi (Broili and Schröder).

Broili, F. and Schröder, J. 1935. *Titanognathus lotzi* Broili and Schröder.

Boonstra, L. D. 1953. *Anteosaurus lotzi* (Broili and Schröder).

Holotype. Skull fragments and some postcranial bones. Alte Akademie, München. No. ?. Brakwater, Beaufort West. Coll. Schröder.

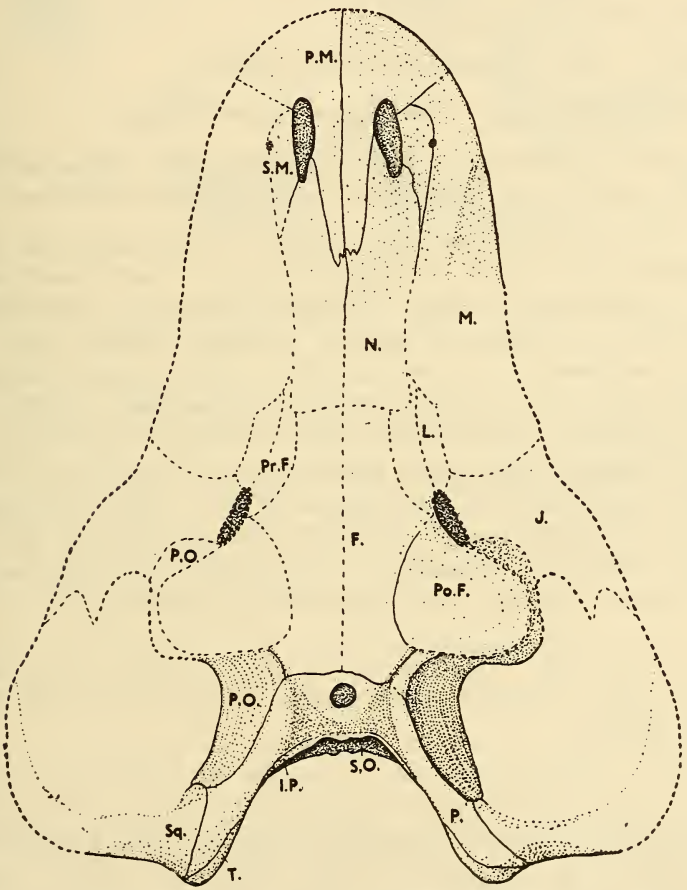

FIG. 7.—*Anteosaurus abeli*. Referred specimen. S.A.M. 11949, Nuwefontein (Roxana), Fraserburg. Dorsal view. This was the first skull in which the truncated posterior limit of the premaxillaries was determined. ($\times \frac{1}{6}$.)

As the type is rather unsatisfactory, consisting of only a fragmentary snout, mandibular fragments, incomplete ilium, pubis and femur, only a very incomplete diagnosis can be given viz.:

Skull size unknown, probably large. Snout length unknown, fairly high and narrow. Intersquamosal width unknown. Postfrontal boss unknown. Jugal boss unknown, angular boss strong. Fronto-naso-prefrontal swelling unknown. Pineal boss unknown. Sharp upward inclination of premaxillary edge, and Broili and Schröder record an accompanying step-up of the precanine border of the dentary. The occiput is unknown. Palate unknown. *Basis cranii* unknown. Condyle unknown. Broili and Schröder give the dental formula $i.\frac{5}{4?}$, $c.\frac{1}{1}$ $p.c.\frac{6}{3+?}$.

Anteosaurus vorsteri (Broom).

Broom, R. 1936. *Dinosuchus vorsteri* Broom.

Boonstra, L. D. 1953. *Anteosaurus vorsteri* (Broom).

Holotype. A good skull and part of the lower jaw. Transvaal Museum. 265. Stinkfontein, Prince Albert. Coll. Vorster, Botes and Broom.

Skull very large; maximum length 740 mm. Snout fairly long, high and wide. Intersquamosal width very great (600 mm.). Size of postfrontal boss unknown, probably fairly strong. Jugal boss unknown, angular boss very strong. Fronto-naso-prefrontal swelling unknown, probably fairly weak. Pineal boss unknown, near? occipital edge. Sharp upward inclination of premaxillary edge. The occiput is high, wide, moderately deeply concave, with a fairly great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch not rising above the plane of the intertemporal surface. Palate fairly long, with deep lateral pterygoidal flanges not massive with sharp ventral edge. *Basis cranii* short, with short basisphenoid. Exoccipitals fused with basioccipital to form a rounded condyle. Broom gives the upper teeth as i.4, c.1, p.c.5.

Referred Specimen. (Figs. 3, 8, 9.) A good skull, but lacking the *basis cranii*. S.A.M. 11577. Bulwater, Beaufort West. Coll. Boonstra and Truter.

Those areas of the outer skull surface lost by weathering in the type specimen are here perfectly preserved and the description of this species can thus be augmented as follows: postfrontal boss fairly strong, but not obscuring the lower part of the postorbital in dorsal view; jugal boss low and small: fronto-naso-prefrontal swelling weak, running evenly on to the anterior nasal surface and with little overhanging of the sides of the skull; pineal boss low, with rounded edges not near occipital edge, with hollow on frontal anterior

to the boss; palatine bosses reniform, not circular as described by Broom; in the left premaxilla stumps of two incisors are preserved and on the right one; for the rest the alveolar border presents a matrix filled groove with little indication of separate alveoli; on the left there appears to be room for 5 and on the right for a total of 4 incisors; on the left alveolar border of the maxilla

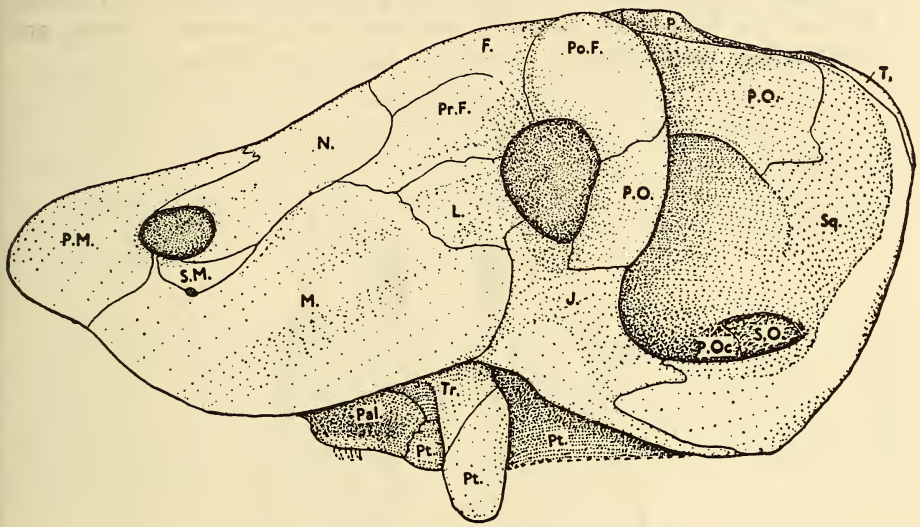

FIG. 8.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Lateral view. ($\times \frac{1}{6}$.)

cross-sections of 7 fairly regular postcanines are seen and on the right 6.

This specimen is of some historical interest in that it was known by the local people to have been exposed when Seeley collected the well-known Tamboerfontein specimen of *Bradysaurus baini*. Weathering is thus not very rapid in the *Tapinocephalus*-zone of the Koup.

Anteosaurus abeli (Boonstra). (Figs. 1, 2, 5, 6, 7.)

Boonstra, L. D. 1952. *Anteosaurus abeli* (Boonstra).

Boonstra, L. D. 1953. *Anteosaurus abeli* (Boonstra).

Holotype. A good skull and lower jaw. S.A.M. 11296. Kruisrivier, Sutherland. Coll. Boonstra.

Skull large, maximum length 700 mm. Snout long, high, moderately wide. Intersquamosal width fairly great (450? mm.). Postfrontal boss fairly large and prominent. Jugal boss low, angular boss very strong. Fronto-naso-prefrontal swelling strong, but only slightly overhanging the sides of the skull. Pineal boss low with rounded edge, situated near occipital

edge. Sharp upward inclination of premaxillary edge. The occiput is high, fairly narrow and deeply concave with a fairly great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises above the plane of the intertemporal surface. Palate probably long. *Basis cranii* unknown. Condyle unknown. In the type there are in the left upper jaw 3 incisors, 1 canine and probably 7 postcanines; whereas on the right side there are 4 incisors, 1 canine and ? postcanines. In the dentary there are 2 incisors on both sides.

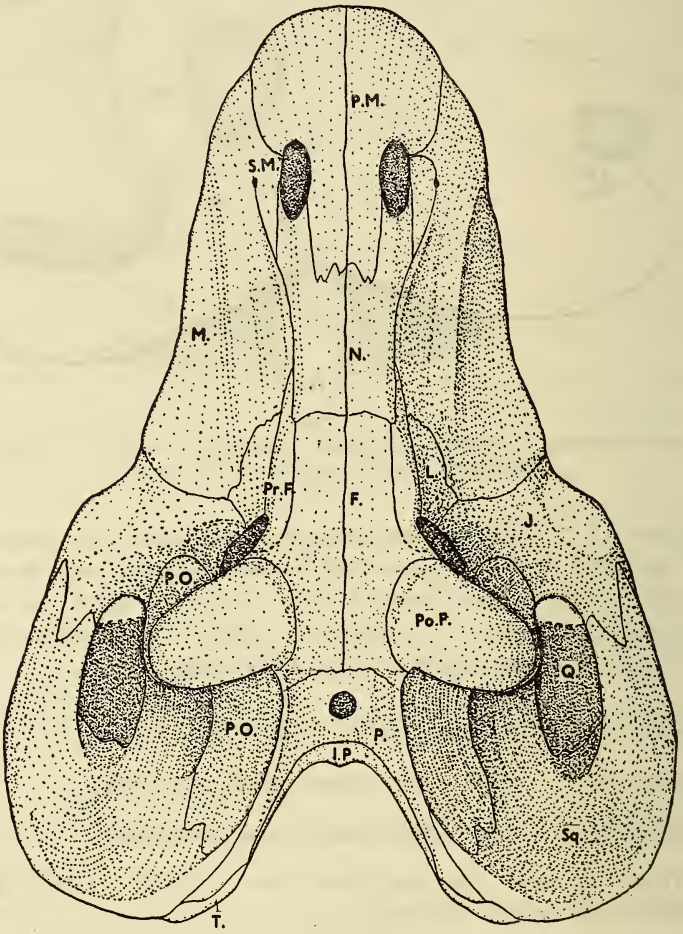

FIG. 9.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Dorsal view. Symmetry restored on the basis of the well preserved left side. ($\times \frac{1}{6}$.)

Paratype. (Fig. 6.) A good skull and parts of the lower jaw. S.A.M. 4340. Leeurivier, Beaufort West. Coll. Haughton.

I have included this specimen in the species — *abeli* — although it differs from the type in a number of points viz. there is only a faint indication of a jugal boss; the frontal enters the supra-orbital border; the premaxilla has a longer alveolar border and on the left carries 5 incisors — the first 4 being very long and strong whereas no. 5 is small and weak; on the left dentary there are 4 long and strong incisors intermeshing with the upper incisors.

S.A.M. 9123 from Voëlfontein, Prince Albert, consists of the major part of a skull which agrees in all essentials with the type skull. Here there are on the left premaxilla 5 cross-sections of incisor roots; these represent numbers 1-4 with a replacing incisor lying median to no. 4. On the right side cross-sections of nos. 2, 3 and 4 are preserved. On the left there is the root of a large canine, whereas on the right there is the empty alveolus of the canine.

S.A.M. 11576 (Fig. 5) from Klein-Koedoeskop, Beaufort West, consists of the anterior part of both jaws. The upper canines are large strongly curved teeth. On the left premaxilla there are 5 incisors — the first 4 long and strong and the fifth short but strong, whereas on the right there are only the 4 anterior incisors. In both dentaries there are 4 incisors — the first 3 long and strong and the fourth much smaller.

S.A.M. 5621, Leeurivier, Beaufort West, consists of two pieces not in contact, representing most of the dorsal surface of a skull, which closely resembles that of the type skull.

S.A.M. .11949 (Fig. 7), Nuwefontein (Roxana), Fraserburg, consists of a snout and the dorsal part of the posterior part of the skull not in contact. This specimen is weathered beautifully white and in the snout the sutures are very clearly shown and it was in this specimen where I first noticed that the premaxillaries were posteriorly abruptly truncated and not long and tapering as in *Jonkeria* and the Tapinocephalids.

Anteosaurus acutirostris Sp. Nov. (Fig. 10.)

Boonstra, L. D. 1953. *Anteosaurus abeli* (Boonstra) in errore.

Holotype. A good skull and lower jaw. S.A.M. 9329, Kruisvlei, Beaufort West. Coll. Boonstra.

Skull large, maximum length 675 mm. Snout long, high, narrow and light. Intersquamosal width great (480? mm.). Postfrontal boss huge and prominent. Jugal boss massive, angular boss massive. Fronto-naso-prefrontal swelling very strong with a distinct step on to the anterior nasal surface and laterally slightly overhanging the sides of the skull. Pineal boss

low with rounded edges extending to the occipital edge. Fairly strong upward inclination of the premaxillary edge. The occiput is high, fairly wide, very deeply concave with a sharp and great posterior sweep of the temporal arches; upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises above the plane of the intertemporal surface. Palate apparently long and narrow. *Basis cranii* fairly long. Exoccipitals fused with basioccipital to form a rounded condyle, which is visible beyond the occipital edge in dorsal view. On both sides there are 4 upper and 4 lower incisors, 1 canine and 5? postcanines. In both dentaries there are 4 incisors.

In this specimen the quadratojugal is clearly seen as a small bone resting on a ledge above the outer quadratic condyle as in the Pristerognathid Therocephalians.

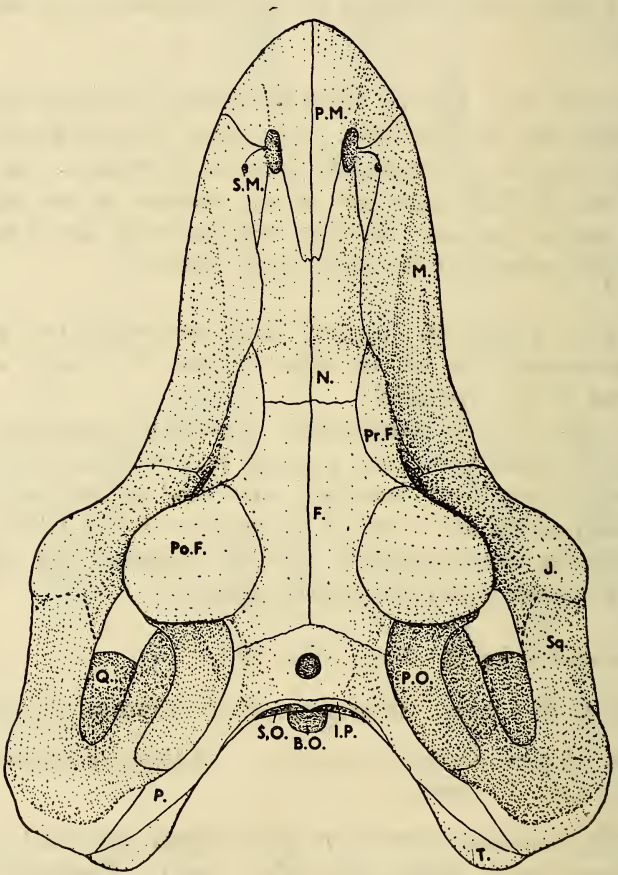

FIG. 10.—*Anteosaurus acutirostris*. Sp. Nov. Holotype. S.A.M. 9329, Kruisvlei, Beaufort West. Dorsal view. Symmetry restored on the basis of the right side, which has suffered a slight side-to-side compression. ($\times \frac{1}{6}$.)

Associated with the holotype skull of *acutirostris* there were a number of skull fragments of other *Anteosaurus* skulls and in addition a large number of bones of the postcranial skeleton of more than one individual. I hope to be able to describe these bones of the postcranial skeleton in the near future. In the meantime a general statement here will be useful.

As a whole the postcranial skeleton is lightly built without any trace of the massiveness so typical of all the hitherto known South African Deinocephalians. One's first impression is that the skeletal bones could belong to some large Therocephalian — associated, for instance, with a skull not very much larger than that of *Scymnosaurus ferox*. This applies particularly to the femur, which is a long bone with the proximal and distal ends hardly expanded and the shaft long and slender.

Anteosaurus crassifrons Sp. Nov. (Figs. 11, 12, 13-

Holotype. A good skull, but distorted by a simple shear. S.A.M. 11946, Buffelsvlei, Beaufort West. Coll. Boonstra and Marais.

Skull large, but short and quat; maximum length 570 mm. Snout short, high and very wide. Intersquamosal width fairly small (330? mm.). Postfrontal boss fairly massive and prominent. Jugal boss massive, angular boss unknown. Fronto-naso-prefrontal swelling very massive with a very distinct step on to the anterior nasal surface and laterally strongly overhanging the sides of the skull. Pineal boss rounded, large and extending on to the frontal. Very sharp upward inclination of the premaxillary edge. The occiput is high, fairly wide, deeply concave, with a great posterior sweep of

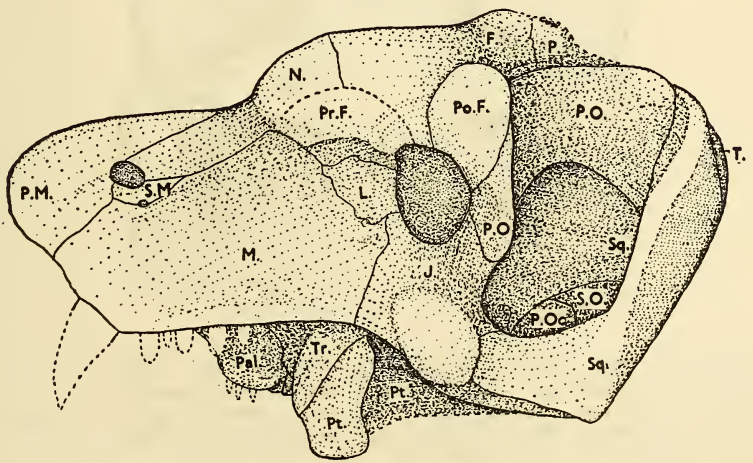

FIG. 11.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Lateral view. ($\times \frac{1}{6}$.)

the temporal arches, and the upper part of the temporal fossa roomy in antero-posterior direction; the temporal arch not rising above the plane of the intertemporal surface. Palate very short with very massive lateral pterygoidal flanges. *Basis cranii* short, with short basisphenoid. Exoccipitals fused with basioccipital to form a rounded condyle. In both premaxillaries no teeth are preserved but 5 matrix-filled alveoli are shown; in both maxillaries 5 postcanine roots of greatly varying diameter are preserved, numbers 2 and 5 being much smaller than the other 3.

S.A.M. 11302 from Buffelsvlei, Beaufort West, is a fairly complete but weathered skull. Although a somewhat larger skull than that of the type, it clearly belongs to the same species. It has the same massive fronto-naso-prefrontal swelling with a distinct step anteriorly and laterally

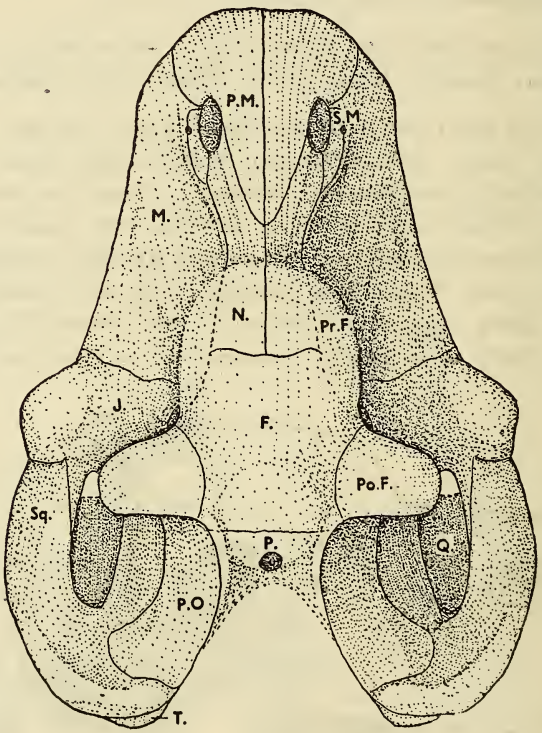

FIG. 12.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Dorsal View. Symmetry affected by a simple shear, restored on the basis of the least affected left side. ($\times \frac{1}{6}$.)

overhanging the preorbital side-wall; the jugal boss is very massive. On the right side there are stumps of 4 incisors and five or six postcanines; a well

preserved crown of a postcanine is of fair size (25 x 14 x 8 mm.); it is a bluntly conical tooth, labio-lingually compressed.

S.A.M. 11929 from an unknown locality, probably near Abrahamskraal, Prince Albert, is an imperfect, weathered skull in extremely intractable matrix, but showing a fairly good ventral surface. The quadrate shows its articular condyles to lie obliquely in the skull with the outer one the more posterior one as shown in reconstruction in all the figures in this paper, and

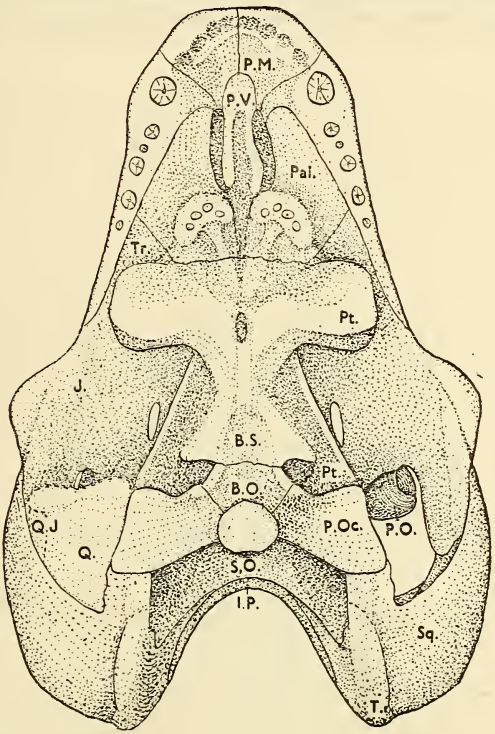

FIG. 13.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Ventral view. Symmetry restored on the basis of the left half of the palate with the result that it is narrower than it would have been in life. On the right the quadrate-complex is indicated in position. (× ⅛.)

thus not as shown in Broom's figure of *Anteosaurus vorsteri*. Part of the left stapes can also be seen and this bone appears to be stout, firmly wedged in the *fenestra ovalis* and abutting against the medial edge of the quadrate dorsal to the extremity of the quadrate ramus of the pterygoid, which appears to overlap the postero-median surface of the quadrate as in *Jonkeria* and the Tapinocephalids. The *basis cranii* is short and wide, with a short basisphenoid. The roots of five postcanines are preserved in the right maxilla.

Anteosaurus major Sp. Nov. (Figs. 14, 15)

Boonstra, L. D. *Anteosaurus abeli* (Boonstra) in errore.

Holotype. A good skull, lacking the snout, but somewhat dorso-ventrally compressed. S.A.M. 11293. Boesmansrivier, Beaufort West. Coll. Boonstra.

Skull very large, maximum length 805? mm. Snout long, fairly broad and high. Intersquamosal width very great (612 mm.). Postfrontal boss

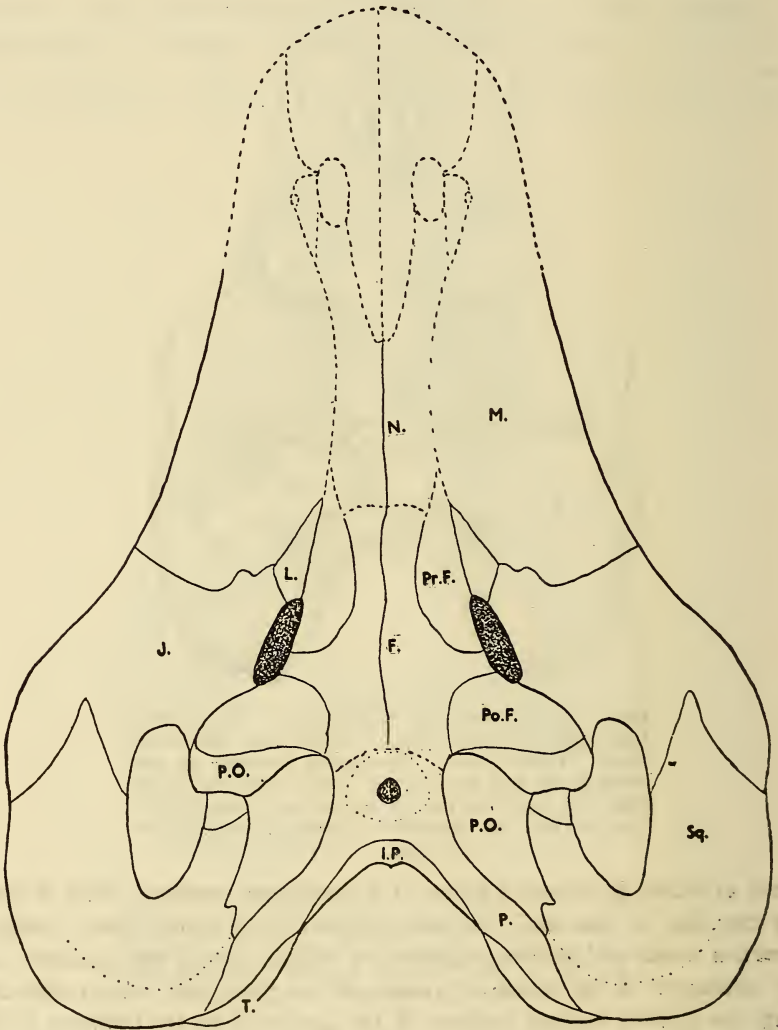

FIG. 14.—*Anteosaurus major*. Sp. Nov. Holotype. S.A.M. 11293, Boesmansrivier, Beaufort West. Dorsal view. Symmetry disturbed by dorso-ventral crushing restored on the basis of the left side. ($\times \frac{1}{6}$.)

only moderately strong and not very prominent, with postorbital forming the postero-lateral part. Low and weak jugal boss, angular boss unknown. Fronto-naso-prefrontal boss moderate, confluent with anterior nasal surface. Pineal boss low, with rounded edges, situated some distance from the occipital edge. Premaxilla unknown. The occiput is low and broad, moderately deeply concave, sweep of temporal arches more laterally than posteriorly and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rising above the level of the intertemporal surface. Palate fairly long

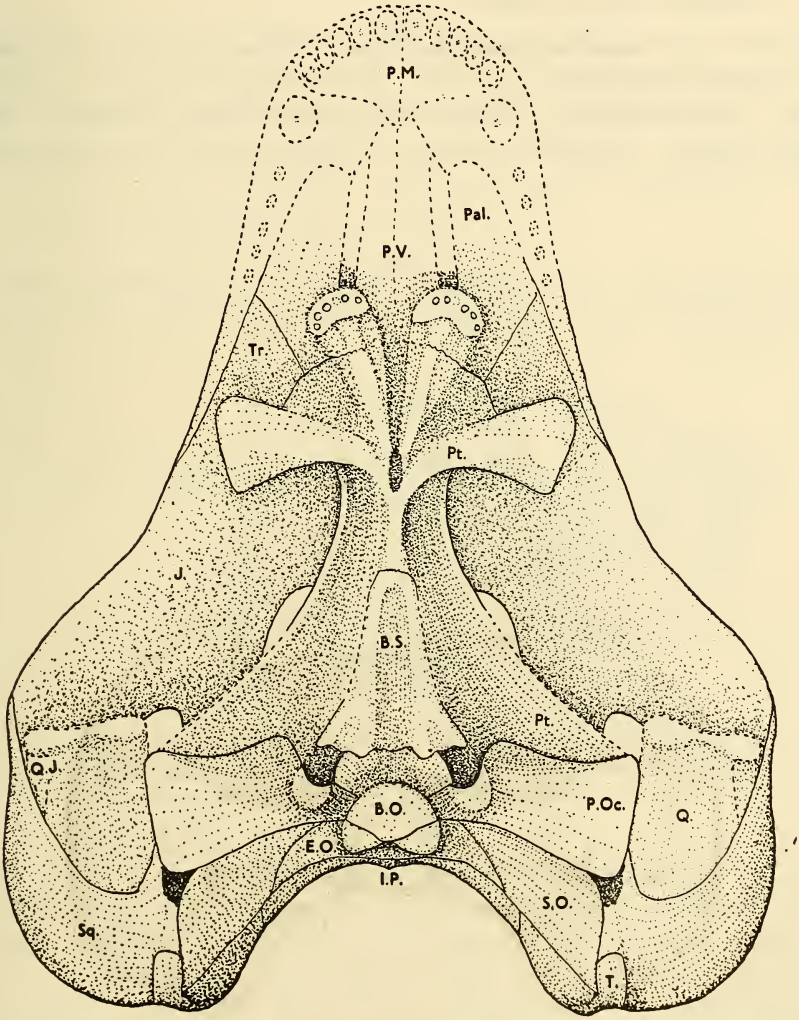

FIG. 15.—*Anteosaurus major*. Sp. Nov. Holotype. S.A.M. 11293, Boesmansrivier, Beaufort West. Ventral view. Symmetry restored on the basis of the left side, which is least disturbed. ($\times \frac{1}{6}$.)

and broad, with strong and deep lateral pterygoidal flanges but not so massive as in *crassifrons*. *Basis cranii* long and basisphenoid much longer than in any of the other species. Exoccipitals forming the dorso-lateral corners of the condyle. No teeth are preserved.

Anteosaurus laticeps Sp. Nov. (Figs. 4, 16)

Holotype. An incomplete skull showing only the ventral and most of the occipital surface. S.A.M. 11592. Dikbome, Laingsburg. Coll. Boonstra and Du Plessis.

Skull large, maximum length 645? mm. Snout short and very broad. Intersquamosal width great (522 mm.). Postfrontal boss unknown. Jugal and angular bosses unknown. Fronto-naso-prefrontal region unknown. Pineal region unknown. Premaxilla unknown. The occiput is low and very broad,

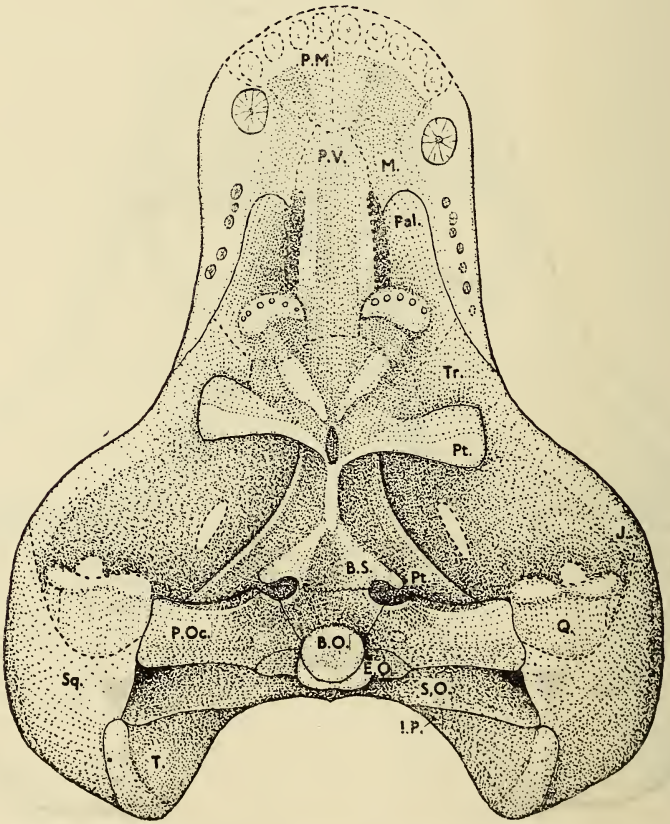

FIG. 16.—*Anteosaurus laticeps*. Sp. Nov. Holotype. S.A.M. 11592, Dikbome, Laingsburg. Ventral view based mainly on the right side. ($\times \frac{1}{6}$.)

shallowly concave; sweep of temporal arches mostly laterally. Palate long and very broad with only moderately strong lateral pterygoidal flanges. *Basis cranii* short, with very short basisphenoid. Exoccipitals forming much of the dorso-lateral corners of the condyle. No incisors are preserved, the canines are very strong, slightly recurved teeth; in the right maxilla stumps of five postcanines can be made out, whereas on the left five teeth are preserved with the probability of another two making a total of 7. The postcanines are bluntly conical, but linguo-labially compressed teeth with the crowns thus oval in crosssection (16 x 11 x 7 mm.).

Anteosaurus cruentus Sp. Nov. (Figs. 17, 18, 19, 20)

Boonstra, L. D. 1953. *Anteosaurus minor* (Broom) in errore.

Holotype. A good, undistorted skull, but lacking the lower jaw. S.A.M. 11694, Koringplaas, Moordenaarskaroo, Laingsburg. Coll. Boonstra and Du Plessis.

Skull moderately large, maximum length 565 mm. Snout long, narrow and fairly low. Intersquamosal width not great (360 mm.). Postfrontal boss

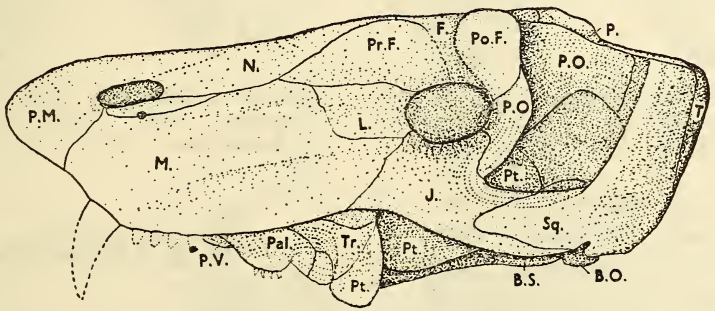

FIG. 17.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Lateral view with the quadrate-complex missing. ($\times \frac{1}{6}$.)

fairly strong and prominent. No jugal boss, angular boss unknown. Fronto-naso-prefrontal swelling small, passing evenly on to the anterior nasal surface. Pineal boss prominent, with sharp circular border, situated very near the occipital edge. Sharp upward inclination of the premaxillary edge. The occiput is high and fairly broad, very deeply concave with a great posterior sweep of the temporal arch and the upper part of the temporal fossa roomy antereo-posteriorly; the temporal arch not rising above the very

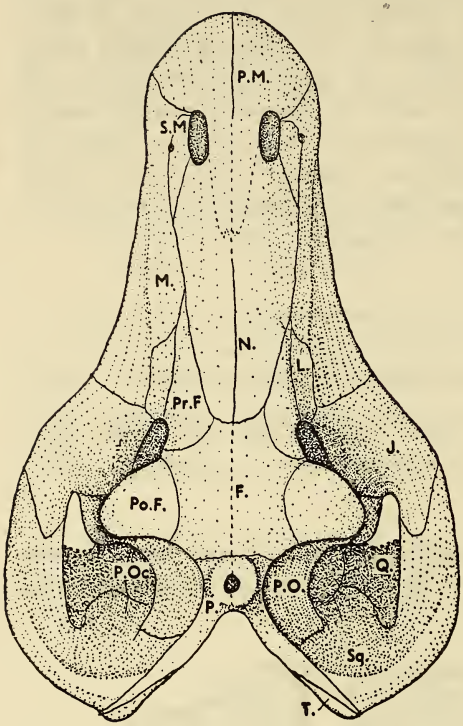

FIG. 18.—*Anteosaurus cruentus*. S. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Dorsal view. (× $\frac{1}{6}$.)

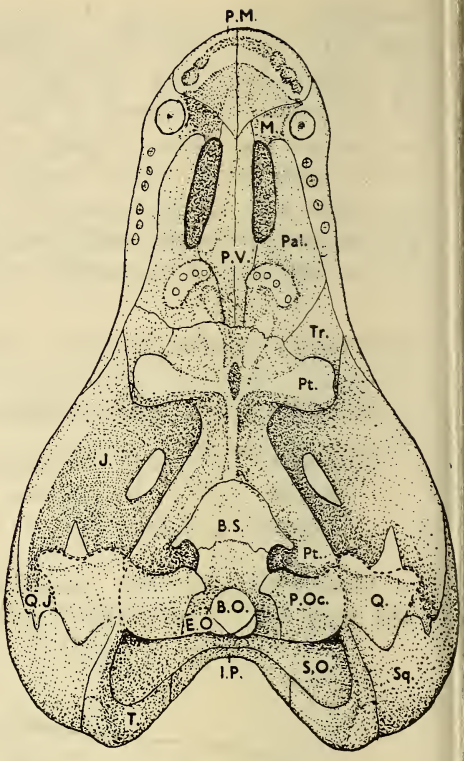

FIG. 19.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Ventral view. (× $\frac{1}{6}$.)

narrow intertemporal surface. Palate long, with fairly robust lateral pterygoidal flanges. *Basis cranii* long, but the basisphenoid is short. The exoccipitals forming a large part of the dorsolateral corners of the condyle. No trace of incisors is preserved; the alveolar face of the premaxillaries shows a matrix filled groove divided in its posterior part into distinct adveoli; there appears to be room for 5 incisors when developed. On the right the canine root is followed by roots of 6 postcanines, but on the left only four roots with a possible fifth can be seen.

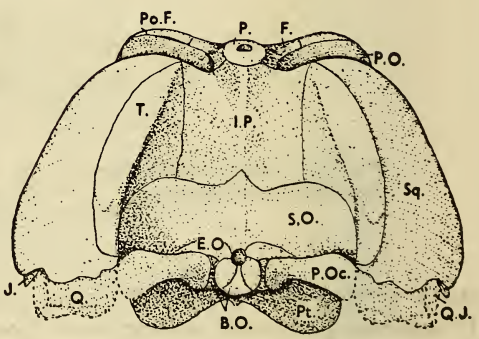

FIG. 20.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Occipital view. (× $\frac{1}{6}$.)

S.A.M. 9140 from Voëlfontein, Prince Albert, is an imperfect disarticulated skull agreeing fairly well with the type, but is of some interest in that it shows a number of the roofbones as separate elements with exposed sutural faces.

Anteosaurus levops Sp. Nov. (Fig. 21)

Holotype. A weathered skull, without the lower jaw. S.A.M. 11492. Mynhardtskraal, Beaufort West. Coll. Boonstra.

Skull fairly small, maximum length 485 mm. Snout fairly short, lightly built, narrow and low. Intersquamosal width relatively large (415 mm.). Postfrontal boss strong and prominent. No jugal boss; angular boss unknown. Fronto-naso-prefrontal swelling strong with a distinct step onto the anterior nasal surface and laterally slightly overhanging the sides of the skull. Pineal boss apparently prominent, reaching the occipital edge. Upward inclination

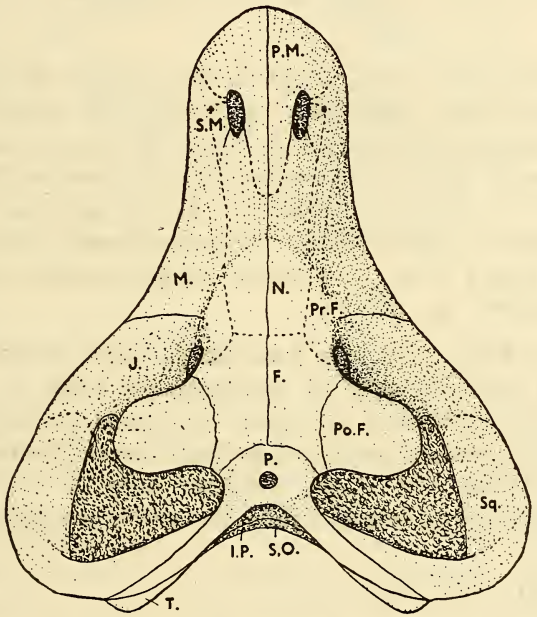

FIG. 21.—*Anteosaurus levops*. Sp. Nov. Holotype. S.A.M. 11492, Mynhardtskraal, Beaufort West. Dorsal view. Temporal fossae not cleared of matrix. ($\times \frac{1}{6}$.)

of the premaxillary edge moderate. The occiput is fairly low and broad; deeply concave, not vertical; strong postero-lateral sweep of the temporal arches and the upper part of the temporal fossa shortened in antero-posterior direction; the temporal arch rising above the plane of the narrow intertemporal

surface. Palate long and narrow. *Basis cranii* fairly short. Condyle unknown. In the right premaxilla parts of the crowns of 3 incisors are preserved, but on the left there is a matrix filled groove with no sign of any teeth.

Anteosaurus minusculus Sp. Nov.

Boonstra, L. D. 1936. *Anteosaurus minor* (Broom) in errore.

Holotype. A distorted skull with the greater part of the arches and most of the palate missing.

American Museum of Natural History, No. 2224. Vanderbylskraal?, Beaufort West. Coll. Broom.

This specimen in the American Museum is stated by Broom to be the topotype of the skull fragment in the British Museum (Natural History) R.5742.

In my paper on the Titanosuchids in the American Museum I attempted a reconstruction of the dorsal aspect of the skull and showed the premaxilla as a long posteriorly tapering bone. With our present knowledge of the truncated posterior end of the premaxilla in all species of *Anteousaurus* this was obviously an error in observation. As this skull has well developed postfrontal bosses it cannot belong to *Pseudanteosaurus minor* (Broom) and I propose to regard it as a new species of *Anteosaurus* under the specific name — *minusculus* sp. nov.

The skull is fairly small with a maximum length of 480 mm.; the snout is long, broad and fairly high; the intersquamosal width was probably small (225? mm.); the postfrontal boss quite strong and prominent; there is no jugal boss; the fronto-naso-prefrontal swelling is weak; the occiput is vertical, very deeply concave with a great posterior sweep of the temporal arches and the upper part of the temporal fossa is roomy in antero-posterior direction.

Anteosaurus sp. (Fig. 22)

S.A.M. 2752, Viviers Siding, Beaufort West. Coll. Haughton and Whaits.

In this specimen we have only the posterior two thirds of the upper surface of a skull. Although it cannot be included in any of the above described species I am not naming it. The skull differs from all the described forms in that the prominent mound-like pineal boss overhangs the occipital surface; the occiput is very deeply concave from side to side with the two horns of the parietal directed nearly wholly in posterior direction; in the posterior

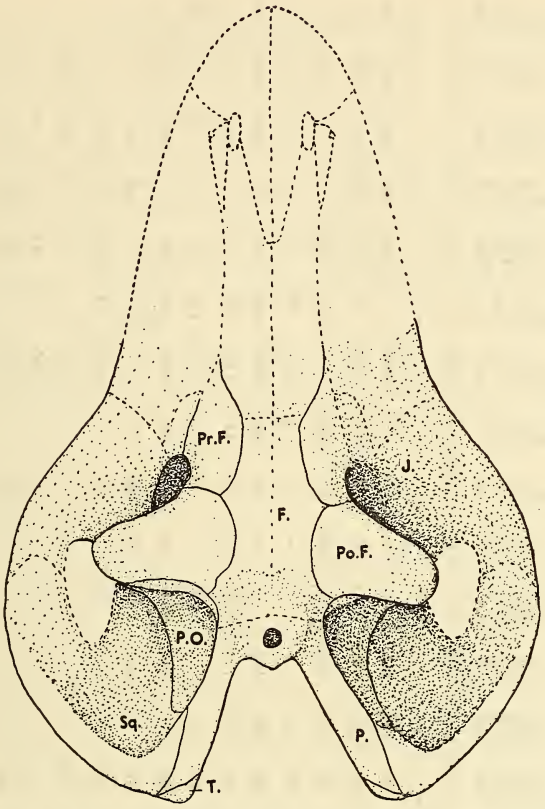

FIG. 22.—*Anteosaurus sp.* S.A.M. 2752, Viviers Siding, Beaufort West. Dorsal View. (× ⅛.)

part of the frontals there is a step bringing this part of the surface down to a lower level than that of the anterior part of the frontals. The postorbitals form a small part of the posterior surface of the boss, whose surface is in other species wholly formed by the postfrontal. These bosses are only moderately strong and prominent. There is very little swelling in the fronto-naso-prefrontal region, but notwithstanding this the prefrontal is so developed to exclude the frontal from entering the supraorbital border.

DISCUSSION

From the above account it is clear that *Anteosaurus* is a genus of the Deinocephalia quite distinct from all the known South African genera. It may be characterised as follows: skull large, with prominent postfrontal bosses; temporal fossa with large dorso-ventral diameter and deep antero-ventral bay; infratemporal bar narrow; quadratojugal no longer lying

CHIEF MEASUREMENTS IN MM.

	A. magnificus B.M.N.H.	*A. lotzi* A.K.	*A. vorsteri* T.M.	*A. vorsteri* S.A.M.	*A. abeli* S.A.M.	*A. abeli* S.A.M.	*A. abeli* S.A.M.	*A. abeli* S.A.M.	*A. crassifrons* S.A.M.	*A. crassifrons* S.A.M.	*A. crassifrons* S.A.M.	*A. acutirostris* S.A.M.	*A. major* S.A.M.	*A. laticeps* S.A.M.	*A. cruentus* S.A.M.	*A. levops* S.A.M.	*A. minusculus* A.M.N.H.
	R 3595	?	265	11577	11296	4340	5621	9123	11946	11302	11929	9329	11293	11592	11694	11492	2224
P.M.—Tab.	660?	750?	740	720	700	680	—	—	570	625	525?	675	805?	645?	565	483	480
P.M.—I.P.	570?	—	581?	600	612	540?	525?	530	460?	535	480?	550	675?	546?	471	396	414
P.M.—Orbit	385?	480?	400?	396	408	363	330?	340	310	340	—	354	465	—	321	270	276
Pin. For.—I.P.	25	—	35?	39	33	—	—	—	—	30	—	30	51	—	15	14	24
Max. Width over Sqs.	360	—	600	528	450	450	—	—	330	330	400?	480	612	522	360	414	222?
Interorbital Width	150	—	145?	120	130	115	135	125	144	147	150	150	132	—	105	108	84
Intertemporal Width	102	—	175?	96	90	—	—	—	81	90	75?	120	87	—	48	69	60
Width over Po. F. bosses	306	—	217?	309	265	275	293	280	270	250	300	291	309	—	210	246	192
Width of snout over Nares	204	136	210?	225	205	200	—	183	210	170	—	171	—	216	141	123	132?
P.M.—B.O.	—	—	636	561?	—	—	—	—	435	—	450?	354	665?	531?	330	—	—
P.M.—Post edge of Lat. Pt. Flange	—	—	385?	360	—	—	—	—	273	—	250?	—	390	354?	303	260?	—
Length of B.S.	—	—	70?	—	—	—	—	—	80?	—	60	—	147	51	50	—	—
Width over Lat. Pt. Flanges	—	—	250?	240	—	—	—	—	210	—	220	—	285	228	162	165?	—

In the case of the forms described by other authors I have included the measurements given by them augumented by measurements taken from their published figures.

on the surface on the latero-postero-ventral corner of the skull but shifted medially as in the higher Therapsids; alveolar border of the premaxilla inclined upwards to give working space to the long, simple, pointed incisors; a short series of postcanine teeth, rather small and irregular; deeply concave occiput; ridge forming the outer border of the occiput proper formed solely by the tabular and squamosal; postorbital covering the lateral face of the parietal and with a long contact with the squamosal; fronto-naso-prefrontal region swollen to a greater or lesser extent; with bosses on the jugal and angular in the larger species; number of incisors variable; great posterior overlap of the maxilla over the jugal.

If the Titanosachia are defined as Deinocephalians with a carnivorous dentition, with quadrate not displaced far anteriorly, with concave occiput, with spacious temporal fossa, then *Anteosaurus* is undoubtedly a Titanosuchian.

The only other S.A. Titanosuchian genus in which the skull is adequately known is *Jonkeria*.

Anteosaurus differs from *Jonkeria* in a number of important points: in *Anteosaurus* the quadratojugal is no longer a surface bone, but has shifted medially (in one species of *Jonkeria* viz. *vanderbyli,* there is an indication that here also there is a similar tendency); in *Anteosaurus* the infratemporal bar is narrow (again *J. vanderbyli* shows a similar tendency); in *Anteosaurus* the temporal fossa extends far ventrally and has in addition an anterior bay of the fossa extending to under the postorbital bar; the postfrontal develops a large boss in *Anteosaurus,* whereas this bone is a small element in *Jonkeria;* large jugal and angular bosses are unknown in *Jonkeria* and the fronto-naso-prefrontal region remains unswollen; the pineal foramen is situated near the occipital edge in *Anteosaurus,* whereas in *Jonkeria* it is situated in the plane of the postorbital bar; in *Jonkeria* the premaxillary edge does not curve sharply upwards; no reniform palatine boss bearing teeth is known in *Jonkeria;* the lateral pterygoidal flanges are much weaker in *Jonkeria;* in *Jonkeria* the posterior sheet of the postorbital does not cover the whole lateral face of the parietal; in *Jonkeria* the jugal is a much smaller bone and does not flare out laterally as it does so characteristically in *Anteosaurus,* nor does it extend so far posteriorly lying along the inner face of the squamosal; in *Jonkeria* the postcanines form a long series, whereas this is short in *Anteosaurus;* the posterior process of the premaxilla in *Jonkeria,* as in the Tapinocephalians, is much longer than in *Anteosaurus;* in *Jonkeria* the ridge on the occiput is formed by the paroccipital, squamosal and tabular, whereas in *Anteosaurus* the paroccipital does not enter into it at all; in *Anteosaurus* the quadrate rami of the pterygoid curve much outwards as they approach the quadrate, whereas in *Jonkeria* they lie nearly parallel to the median line; in *Anteosaurus* the stapes is a much longer bone; in

Anteosaurus the maxilla has a much greater overlap over the jugal. These differences, together with others not listed here, to my mind show that these two genera lie on lines of development sufficiently divergent to warrant our placing them in different families, which I propose to name the *Anteosauridae* and the *Jonkeridae*.

It is thus clear that the Anteosauridae, although retaining a number of primitive characters, have advanced farther in some points of structure than their contemporaries the Jonkeridae.

Comparison with Other Therapsids

In South Africa the Therapsids are first encountered in the *Tapinocephalus-zone*. With its complex of monoclinal folds it has up to the present not been possible to establish from what level within the zone the various known Therapsid finds have come. Until then we are forced to consider the assemblage of forms from this zone as being contemporaneous.

The thus contemporary Therapsids from the *Tapinocephalus*-zone are: Anningiamorpha, Dromasauria, Anomodontia, Gorgonopsia, Therocephalia and Deinocephalia. These are all present as well established groups clearly distinct from each other.

The Anningiamorphs are not very well known, but appear to be a group in which a large number of primitive characters have persisted.

The Dromasaurians are only known from four specimens and combine a number of primitive characters with some rather specialised.

The Anomodonts, although but poorly represented in this zone compared to the great diversity developed in the younger rocks of the Karroo, are already quite specialised when they are first encountered. No group with such a remarkable edentulous premaxilla can be anything but firmly set on an independent line of development.

The Gorgonopsians, with but a few forms present in the *Tapinocephalus*-zone, blossomed exceedingly in later ages, but the oldest known species are already definite Gorgonopsians with a habitus well established and clearly their own and the subsequent developments in no way exceeded the limitations inherent in these early forms from the *Tapinocephalus*-zone.

The Therocephalians of the *Tapinocephalus*-zone are a virile suborder of the Therapsids already represented by a large number of species, which, representing different lines of development, can be placed in a number of different families. Having already, by the beginning of the *Tapinocephalus*-zone times, split into a number of families it is clear that the tempo of development within the suborder during the antecedent ages must have been greater than in the Gorgonopsians. This was probably due to a greater lability in the original stock. As their successors — not only the higher Therocephalian families but also their off-spring the Cynodonts, Bauriamorphs

and Ictidosaurians, of the later Karroo Beds — show, this lability or greater potentiality for further development beyond the confines of the suborder was maintained.

The Deinocephalians, when first encountered in the *Tapinocephalus*-zone, were already at the end of their tether. They are represented by the end-products of their particular line of development which culminated in the 3 specialised groups — Titanosuchia, Tapinocephalia and Styracocephalia.

Characters of a Postulated Primitive Therapsid Ancestor

If we postulate a primitive Therapsid ancestor, common to all the Therapsids, situated on a morphological level somewhere between that of the early Pelycosaurs and the first Therapsids we would expect it to have the following characters: intertemporal region broad and flat; preparietal absent; premaxilla without long posterior process intercalated between the nasals; the postfrontal well developed; the postorbital covering the lateral face of the parietal and meeting the squamosal; the pineal foramen well in advance of the occipital edge i.e. the upper occipital edge has not yet migrated anteriorly; the premaxilla below the nostril would still be shallow; the zygomatic arch shallow; the temporal fossa relatively small with the squamosal not bowing out laterally or posteriorly; the quadratojugal still lying on the outer surface i.e. not yet migrated internal to the squamosal; the occiput low, fairly narrow, vertical, with its upper border not moved anteriorly, not deeply concave from side to side; the paroccipital just beginning to strengthen and to support the quadrate; the quadrate would still be large with its condyle lying fairly far ventrally, but still in the posterior position i.e. in line with the occipital condyle; the premaxilla would be dentigerous and with hardly any palatal face; the maxillary teeth would form a long series and there would probably already be a specialised canine; choanae and nares anteriorly situated; no suborbital opening; the lateral pterygoidal processes would still be situated fairly far back and be fairly weak; the basisphenoid-pterygoid joint would no longer be movable and the contact of the basisphenoid with the pterygoid shifted posteriorly; the basisphenoid processes flattening; the quadrate ramus of the pterygoid reduced in height; the parasphenoidal rostrum would still be visible in the posterior part of the interpterygoidal slit; there would be no coronoid process to the dentary; the lower jaw long and the angular notch and reflected lamina would be beginning to develop.

Tabulating the characters of the Therapsids of the *Tapinocephalus*-zone on the basis of the above list one gets the following result:

The Anningiamorpha are not sufficiently well known to make a count of the characters corresponding with those in the above list, but those preserved

point to this group as approaching the postulated primitive Therapsid condition most closely.

The Dromasauria, as far as they are known, appear to occupy the second place.

Then come the three groups of the Deinocephalia — which, although clearly distinct from each other — due to particular specialisation — seem to stand on more or less the same morphological level.

Somewhat further removed from the postulated primitive Therapsid condition are the Dicynodonts, and then come the Gorgonopsians, followed by the Therocephalians in which the rate of development away from the primitive Therapsid condition has been the greatest.

Finally, *Anteosaurus* has advanced beyond the primitive Therapsid stage in the following characters: the premaxilla, below the nostril has increased in depth and then the alveolar edge has curved upwards; the temporal fossa has become very roomy and the squamosal is bowed out strongly both laterally and posteriorly; the quadratojugal has migrated from the outer surface to lie medial of the zygoma; the occiput has greatly increased its surface by becoming both broad and high; the paroccipital process has become very strong and supports the quadrate firmly; the length of the postcanine series has decreased and the long incisors have become intermeshing teeth; the lateral pterygoidal processes are situated well forward and are very strongly developed; the basisphenoid-pterygoid region has advanced as in higher Therapsids, but there are no strong basisphenoidal tubera and lastly we have the characteristic pachyostosis with the development of the peculiar postfrontal, jugal and angular bosses.

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